

Visual decisions in the presence of measurement and stimulus correlations

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Abstract

Humans and other animals base their decisions on noisy sensory input. Much work has therefore been devoted to understanding the computations that underly such decisions. The problem has been studied in a variety of tasks and with stimuli of differing complexity. However, the impact of correlations in sensory noise on perceptual judgments is not well understood. Here we examine how stimulus correlations together with correlations in sensory noise impact decision making. As an example, we consider the task of detecting the presence of a single or multiple targets amongst distractors. We assume that both the distractors and the observer's measurements of the stimuli are correlated. The computations of an optimal observer in this task are nontrivial, yet can be analyzed and understood intuitively. We find that when distractors are strongly correlated, measurement correlations can have a strong impact on performance. When distractor correlations are weak, measurement correlations have little impact, unless the number of stimuli is large. Correlations in neural responses to structured stimuli can therefore strongly impact perceptual judgments.

1 Introduction

The perceptual system has evolved to extract ecologically meaningful information from sensory input. For example, in many mid- to high-level visual tasks the brain has to make categorical, global judgements based on multiple stimuli where the identity of any individual stimulus

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is not of direct relevance. In a visual search task, the goal might be to detect whether a predefined target object is present in a scene that contains multiple objects. Complicating such tasks is the fact that noise corrupts sensory measurements, especially when observation time is short, or many objects are present.

Much work has been devoted to modeling the decision processes by which the brain converts noisy sensory measurements of a set of stimuli into a judgement about a global world state, such as the presence or absence of a target. These models often focus on various decision rules that can be applied to the measurements. By contrast, the measurements themselves are usually modeled in a rather stereotypical fashion, namely as independent and normally distributed, (e.g. Peterson et al. (1954); Nolte and Jaarsma (1967); Pelli (1985); Graham et al. (1987); Palmer et al. (1993); Baldassi and Burr (2000); Baldassi and Verghese (2002); van den Berg et al. (2012); Ma et al. (2011); Mazyar et al. (2012)). Both the assumption of independence and the assumption of Gaussianity can be questioned. Specifically, neural correlations can extend to distances as long as 4mm in monkey cortex (Ecker et al., 2010; Cohen and Kohn, 2011). This suggests that sensory measurements can be strongly correlated (Rosenbaum et al., 2010; Chen et al., 2006). Here we focus on the effects of violation of the assumption of independent measurements on performance in categorical, global perceptual judgements.

To make such perceptual judgments, an observer needs to take into account the statistical structure of the stimuli *and* the structure of measurements. Consider a search task where a subject is required to detect a target among distractors. The effects of measurement correlations and stimulus correlations will be intertwined: If the distractors are identical on a given trial, then strong correlations between the measurements will help preserve their perceived similarity. Namely, an observer can group the distractor measurements and identify the target as corresponding to the outlying measurement. By contrast, when distractors are unstructured (independently drawn across locations), strong measurement correlations may have no effect on performance. Thus, measurement and stimulus correlations should not be considered in isolation.

Here we examine how measurement and stimulus correlations impact the strategy and the performance of an ideal observer in a target detection task. We assume that on half the trials, one or more target stimuli are presented along with a number of distractors, whereas on the other half of trials, only distractors are presented. The task is to infer whether targets are present or not. Importantly, we assume that the distractor stimuli are not drawn independently – for instance, in the extreme case the targets could be identical. Our ideal observer infers target presence based on measurements of the stimuli. We assume that these measurements are corrupted by *correlated* noise. In an extreme case, this noise is perfectly correlated and all measurements are perturbed by the same, random value.

We provide an analytical study of the optimal decision rule to show that the interplay of measurement and stimulus correlations can be intricate. In general, if the stimuli are strongly correlated, then measurement correlations can strongly affect the performance of an ideal observer. When stimuli are weakly correlated, measurement correlations have a smaller impact.

We expect that these insights hold more generally: Natural stimuli are structured, and their distributions are concentrated along low dimensional structures in stimulus space (Geisler,

2008). Correlations in measurement noise could thus help in the inferring parameters of interest. Ultimately, we thus expect our results to be relevant to modeling perceptual decision-making in natural scenes.

2 Model description

To examine how decisions of an ideal observer are determined by the statistical structure of measurements and stimuli we consider the following task. An observer is asked whether target stimuli are present among a set of distractor stimuli. Each stimulus, i , is characterized by a scalar, $s_i \in \mathbb{R}$. The set of N stimuli presented on a single trial is characterized by the vector $\mathbf{s} = (s_1, s_2, \dots, s_N)$. For instance, stimuli could be pure tones characterized by their frequency, gratings characterized by their orientation, or ellipses characterized by the orientation of their major axis. A *target* is a stimulus with a particular characteristic, s_T . A target could be a vertical grating, or a pure tone at 440Hz. For simplicity, we assume that, if i is a target, then $s_i = s_T = 0$, and stimulus characteristics are measured relative to that of a target. Stimuli that are not targets are distractors. For such stimuli $s_j \neq 0$ with probability 1. We will consider situations with single and multiple targets.

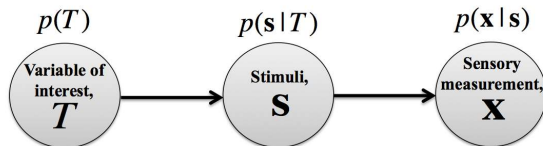


Figure 1: A schematic representation of Bayesian inference. Information about a parameter of interest, T , is encoded in a stimulus vector, \mathbf{s} . The dimension of \mathbf{s} could be much higher than the dimension of T . The observer makes a sensory measurement, \mathbf{x} , of the stimulus, \mathbf{s} , and must infer T from this measurement. This inference requires marginalization over \mathbf{s} .

The following treatment parallels the one we used earlier for independent measurements (Mazur et al., 2012, 2013; Bhardwaj et al., 2015). We denote target presence by $T = 1$, and absence by $T = 0$. We assume that targets are present with probability 0.5. When $T = 0$ (no targets) stimuli are drawn from a multivariate normal distribution with mean $\mathbf{0}_N = (0, 0, \dots, 0)$, and covariance matrix, $\Sigma_{\mathbf{s}}$. The subscript denotes vector length, so $\mathbf{0}_N$ has N components. We can therefore write

$$p(\mathbf{s}|T) = \mathcal{N}(\mathbf{s}; \mathbf{0}_N, \Sigma_{\mathbf{s}}), \quad (2.1)$$

where $\mathcal{N}(\mathbf{s}; \boldsymbol{\mu}, \Sigma)$ denotes the density of the normal distribution with mean $\boldsymbol{\mu}$ and covariance Σ . For simplicity, we assume $\Sigma_{\mathbf{s}}$ has constant diagonal and off-diagonal terms, so that

$$\Sigma_{\mathbf{s}} = \sigma_s^2 \begin{bmatrix} 1 & \rho_s & \cdots & \rho_s \\ \rho_s & 1 & \cdots & \rho_s \\ \vdots & & \ddots & \vdots \\ \rho_s & \rho_s & \cdots & 1 \end{bmatrix}. \quad (2.2)$$

The correlation coefficient, ρ_s , determines the relation between the components of the stimulus.

If $T = 1$, then $n \geq 1$ targets are present. In this case we assign, with uniform probability, the target characteristic to n out of the total of N stimuli. This subset n targets is denoted by L . We denote by \mathcal{L} the collection of all $\binom{N}{n}$ possible choices of the sets L of targets.

The remaining $N - n$ distractors are drawn from a multivariate normal distribution with mean $\mathbf{0}_{N-n}$, and covariance matrix $\Sigma_{\mathbf{s}_{\setminus L}}$ of dimension $(N - n) \times (N - n)$. Let $\mathbf{s}_L = (s_{i_1}, s_{i_2}, \dots, s_{i_n})$, $i_l \in L$ denote the target stimuli, and $\mathbf{s}_{\setminus L} = (s_{j_1}, s_{j_2}, \dots, s_{j_{N-n}})$, $j_l \notin L$ the distractors. We can therefore write

$$p(\mathbf{s}_L | T = 1) = \sum_{i \in L} \delta(s_i), \quad \text{and} \quad p(\mathbf{s}_{\setminus L} | T = 1) = \mathcal{N}(\mathbf{s}_{\setminus L}; \mathbf{0}_{N-n}, \Sigma_{\mathbf{s}_{\setminus L}}).$$

Since the density $p(\mathbf{s} | T = 1, L)$ is singular, we introduce the auxiliary covariance,

$$(\Sigma_{\mathbf{s}, L}^\eta)_{i,j} = \begin{cases} (\Sigma_{\mathbf{s}_{\setminus L}})_{i,j}, & \text{if } i, j \notin L, \\ \eta, & \text{if } i = j \in L, \\ 0, & \text{if } i \in L, \text{ or } j \in L, \text{ and } i \neq j, \end{cases} \quad (2.3)$$

where $\eta > 0$. Therefore,

$$p(\mathbf{s} | T = 1, L) = \lim_{\eta \downarrow 0} \mathcal{N}(\mathbf{s}; \mathbf{0}_N, \Sigma_{\mathbf{s}, L}^\eta).$$

We further assume that an observer makes a noisy measurement, x_i , of each stimulus, s_i . This measurement can be thought of as the estimate of stimulus i obtained from the activity of a population of neurons that responded to the stimulus. We denote by $\mathbf{x} = (x_1, x_2, \dots, x_N)$ the vector of N measurements. It is commonly assumed that these measurements are unbiased, and corrupted by additive, independent, normally distributed noise, so that $p(\mathbf{x} | \mathbf{s}) = \prod_{i=1}^N \mathcal{N}(x_i; s_i, \sigma_x^2)$. Here we consider the more general situation where the measurements are unbiased, but noise could be correlated so that

$$p(\mathbf{x} | \mathbf{s}) = \mathcal{N}(\mathbf{x}; \mathbf{s}, \Sigma_{\mathbf{x}}). \quad (2.4)$$

We consider the particular case when $\Sigma_{\mathbf{x}}$ has constant diagonal terms, σ_x^2 , and off-diagonal terms, $\rho_x \sigma_x^2$, so that

$$\Sigma_{\mathbf{x}} = \sigma_x^2 \begin{bmatrix} 1 & \rho_x & \cdots & \rho_x \\ \rho_x & 1 & \cdots & \rho_x \\ \vdots & & \ddots & \vdots \\ \rho_x & \rho_x & \cdots & 1 \end{bmatrix}. \quad (2.5)$$

Note that

$$p(\mathbf{x} | T = 1) = \int p(\mathbf{x} | \mathbf{s}) p(\mathbf{s} | T = 1) d\mathbf{s},$$

and similarly for $p(\mathbf{x} | T = 0)$. We must thus marginalize over \mathbf{s} to obtain these distributions. A simple computation (See Appendix A) shows that $p(\mathbf{x} | L, T = 1) = \mathcal{N}(\mathbf{x}; \mathbf{0}_N, \Sigma_{\mathbf{s}, L}^0 + \Sigma_{\mathbf{x}})$, and $p(\mathbf{x} | T = 0) = \mathcal{N}(\mathbf{x}; \mathbf{0}_N, \Sigma_{\mathbf{s}} + \Sigma_{\mathbf{x}})$.

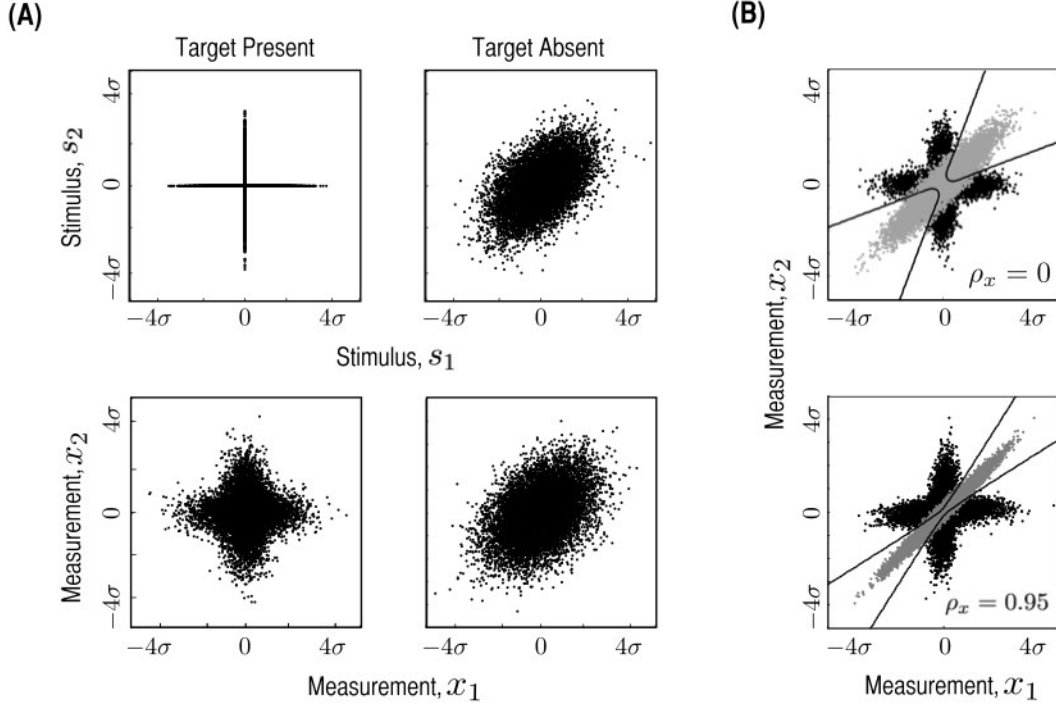


Figure 2: Stimulus and measurement distributions in the single target detection task with $N = 2$ stimuli and $\sigma_s = 15, \sigma_x = 4$. **(A)** (Top) Stimulus distributions on target present (left) and target absent (right) trials for $\rho_s = 0.5$. On target present trials, the distribution is constrained to the axes, since one of the stimuli is a target. On target absent trials, the two stimuli follow a bivariate normal distribution. (Bottom) Distributions of measurements in the absence of measurement correlations, $\rho_x = 0$. On both the target present (left), and target absent case (right), the measurement distribution inherits its shape from the stimulus distribution. **(B)** Overlap of measurement distributions for strongly correlated distractors, $\rho_s = 0.99$. Measurement distributions on target present (black) and absent (gray) trials are shown for $\rho_x = 0$ (top) and $\rho_x = 0.95$ (bottom). The overlap between the measurement distributions decreases with increasing measurement correlation, ρ_x . The decision boundary (solid line) therefore better separates the two distribution when ρ_s and ρ_x are both large. We used high correlations to bring out the difference between the distributions. Axes represent the total standard deviation of the measurements, $\sigma = \sqrt{\sigma_s^2 + \sigma_x^2}$.

3 Results

Our goal is to describe how correlations between stimuli along with correlations between their measurements affect the decisions of an optimal observer in a target detection task. We examine how performance changes as both correlations between distractors and between measurements are varied.

The stimuli, \mathbf{s} , follow different distributions depending on whether $T = 0$ or $T = 1$. Measurement noise increases the overlap between the corresponding measurement distributions, $p(\mathbf{x}|T = 0)$ and $p(\mathbf{x}|T = 1)$. The higher the overlap between these two distributions, the more difficult it is to tell whether a target is present or not. However, correlations in measurement noise can reduce such overlap (See Fig. 2B), even when noise intensity is unchanged. Therefore, the estimate of a parameter from a neural response depends not only on the level, σ_x , but also on the structure of measurement noise (Abbott and Dayan, 1999; Sompolinsky et al., 2001; Averbeck et al., 2006; Josić et al., 2009).

An ideal observer makes a decision based on the sign of the log posterior ratio,

$$d_{\text{TD}}(\mathbf{x}) = \log \frac{p(T = 1|\mathbf{x})}{p(T = 0|\mathbf{x})} = \log \frac{p(\mathbf{x}|T = 1)}{p(\mathbf{x}|T = 0)} + \log \frac{p(T = 1)}{p(T = 0)}. \quad (3.1)$$

If $d_{\text{TD}}(\mathbf{x}) > 0$, the observer infers that a target is present. Note that

$$p(\mathbf{x}|T = 1) = \sum_{L \in \mathcal{L}} p(\mathbf{x}|L, T = 1)p(L).$$

Given that the prior probability that L is a set of targets is uniform gives $p(L) = \binom{N}{n}^{-1}$, and

$$d_{\text{TD}}(\mathbf{x}) = \log \frac{p(\mathbf{x}|T = 1)}{p(\mathbf{x}|T = 0)} = \log \left[\binom{N}{n}^{-1} \sum_{L \in \mathcal{L}} \frac{p(\mathbf{x}|L, T = 1)}{p(\mathbf{x}|T = 0)} \right]. \quad (3.2)$$

The decision variable thus depends on the sum of the normalized probabilities that a measurement in \mathbf{x} is made, given that the target set is L .

Note also that

$$p(L|\mathbf{x}, T = 1) \propto p(\mathbf{x}|L, T = 1).$$

Therefore, the decision variable can also be interpreted as a sum of likelihoods that L is a target set, given a measurement \mathbf{x} . Thus the decision is directly related to the posterior distribution over the target sets L : The summands in Eq. (3.2) correspond to the evidence that L is a set of targets.

The distribution of measurements, \mathbf{x} , depends on whether a target or targets are present. The conditional distributions of measurements, $p(\mathbf{x}|T = 0)$ and $p(\mathbf{x}|L, T = 1)$, are Gaussian with all means equal to 0, and covariances $\mathbf{C} = \Sigma_s + \Sigma_x$ and $\mathbf{C}_L = \Sigma_{s,L}^0 + \Sigma_x$, respectively. We therefore have (see Appendix A for details)

$$d_{\text{TD}}(\mathbf{x}) = \log \left[\binom{N}{n}^{-1} \sqrt{\frac{|\mathbf{C}|}{|\mathbf{C}_L|}} \sum_{L \in \mathcal{L}} \exp \left(-\frac{1}{2} \mathbf{x}^T (\mathbf{C}_L^{-1} - \mathbf{C}^{-1}) \mathbf{x} \right) \right]. \quad (3.3)$$

This decision variable depends on the model parameters, and the measurement, \mathbf{x} . The total number of stimuli, N , number of targets, n , and the variability, σ_s^2 . The correlation, ρ_s , between the distractors determine the structure of the stimulus, while the variability, σ_x^2 , and correlation, ρ_x , describe the distribution of sensory measurements. An ideal observer knows all these parameters.

Setting the right hand side of Eq. (3.3) to 0 defines a nonlinear decision boundary in the space of measurements. This boundary separates measurements that lead to a “target present” decision ($d_{\text{TD}}(\mathbf{x}) > 0$) from those that lead to a “target absent” decision ($d_{\text{TD}}(\mathbf{x}) < 0$). For example, with a single stimulus, $N = n = 1$, the observer needs to decide whether or not a single measurement corresponds to a target. The decision variable has the form

$$d_{\text{TD}}(\mathbf{x}) = \log \left(\sqrt{\frac{\sigma_s^2 + \sigma_x^2}{\sigma_x^2}} \right) - \frac{1}{2\sigma_x^2} \frac{x_1^2}{1 + \sigma_x^2/\sigma_s^2},$$

If the measurement, x_1 , differs sufficiently from 0, then $d_{\text{TD}}(\mathbf{x}) < 0$. A measurement close to 0, gives $d_{\text{TD}}(\mathbf{x}) > 0$.

With more stimuli, the observer needs to take into account the known correlations between the stimuli and between the measurements. The decision variable depends in a complicated way on the parameters that describe the structure of the stimulus and the response. The explicit form of Eq. (3.3), can be derived under the assumption of equal variances and equal covariances (See Appendix A)

$$d_{\text{TD}}(\mathbf{x}) = \log \left(\frac{1}{M} \sqrt{\frac{1 + (\rho_s \sigma_s^2 + \rho_x \sigma_x^2) N v}{\gamma_L}} \left(\frac{v_L}{v} \right)^n \sum_{L \in \mathcal{L}} \exp \left\{ -\frac{1}{2} \left(\underbrace{\sigma_s^2 (1 - \rho_s) v_L v \sum_{i \in L} x_i^2}_{\text{I}} \right. \right. \right. \\ \left. \left. \left. + \underbrace{\left(\beta v^2 - \frac{\rho_x \sigma_x^2 v_L^2 g_L}{\gamma_L} \right) \sum_{i,j \in L} x_i x_j}_{\text{II}} + 2 \underbrace{\left(\beta v^2 - \frac{\rho_x \sigma_x^2 v_L v}{\gamma_L} \right) \sum_{i \in L, j \notin L} x_i x_j}_{\text{III}} + \underbrace{\left(\beta v^2 - \frac{v^2 f_L}{\gamma_L} \right) \sum_{i,j \notin L} x_i x_j}_{\text{IV}} \right\} \right) \right). \quad (3.4)$$

The variables v and v_L represent scaled inverse variances corresponding to distractor and target stimuli. The parameters β, g_L, f_L , and γ_L are given in Eqs. (A.4) and (A.5), and are defined in terms of $\sigma_s^2, \rho_s, \sigma_x^2$, and ρ_x . Eq. (3.4) has a form that can be interpreted intuitively:

1. Term I contains a sum of squares of individual measurements, x_i^2 , over the putative set of targets, L . The smaller this sum, the more likely that L contains targets.
2. Term II contains the sample covariance about the known target value, $s_T = 0$, that is, $\sum_{i,j \in L} (x_i - s_T)(x_j - s_T) = \sum_{i,j \in L} x_i x_j$. In the absence of measurement correlations, $\rho_x = 0$, covariability about the target value has vanishing expectation for target measurements. Therefore the larger this sum, the less likely that the measurements come from a set of target stimuli. In the presence of measurement correlations, $\rho_x > 0$, covariability between target measurements is expected. Hence the prefactor in term II decreases with ρ_x .

3. Term III is similar to term II, with the sum representing the sample covariance about the target value between putative target and non-target stimuli. The larger this covariance, the less likely that L or its complement contain targets.
4. Term IV contains the sample covariance about the mean of measurements outside of the putative target set. If there are no targets, then all terms in the sum are expected to be large, regardless of the choice of L . However, if there are targets, then whenever the complement of L contains targets, some of the terms in the sum have expectation 0. Hence the term again makes a smaller contribution if targets are present.

While this provides an intuitive interpretation of the sums in Eq. (3.4), the expression is complex and it is difficult to precisely understand how an ideal observer uses knowledge of the generative model and the stimulus measurements to make a decision. We therefore examine a number of cases where Eq. (3.4) is tractable, and all the terms can be interpreted precisely. We also numerically examine performance in a wider range of examples.

3.1 Single target, $n = 1$

We start with the case when a single target is present at one of N locations. This case was considered previously in the absence of correlations between the sensory measurements (Bhardwaj et al., 2015).

We observe in Figs. 3A and 4A that the performance of an ideal observer is nearly independent of ρ_s and ρ_x when external structure is weak ($\rho_s < 1$). Performance depends strongly on ρ_x when distractors are strongly correlated, $\rho_s \approx 1$. An ideal observer performs perfectly when $\rho_s = \rho_x = 1$ (Fig. 3C).

Increased performance with increasing stimulus correlations, ρ_s , accords with intuition that similar distractors make it easier to detect a target. However, correlations in measurement noise can play an equally important role and significantly improve performance when distractors are identical (See Fig. 3B).

Perfect performance when $\rho_s = \rho_x = 1$, can be understood intuitively. In this case measurements, x_i , of the stimuli are obtained by adding the *same* realization of a random variable, *i.e.* identical measurement noise to each stimulus value, s_i . In target absent trials, all measurements are hence identical. If the target is present, measurements contain a single outlier. An ideal observer can thus distinguish the two cases perfectly.

We examine in more detail the cases of weak measurement noise, and then the case of comparable measurement noise and distractor variability.

Weak measurement noise, $\sigma_x^2 \ll \sigma_s^2$ with highly correlated stimuli, $\rho_s \approx 1$. When measurement noise is weak, discriminability between the “target absent” and “target present” conditions is governed by external variability, *i.e.* trial-to-trial variability of the stimuli. As noted, measurement correlations improve discriminability in the presence of strong stimulus correlations (see Figs. 3A,C). When $\rho_s \approx 1$, Eq. (3.4) can be approximated as (details in

Appendix B.1):

$$d_{\text{TD}}(\mathbf{x}) \approx \log \left(\underbrace{\frac{1}{N} \sqrt{\frac{N(1-\rho_x)}{N-1}}}_{P(N, \rho_x)} \sum_{i=1}^N \exp \left\{ \underbrace{-\frac{1}{2N\sigma_x^2(1-\rho_x)} \left((1-N\rho_x)x_i^2 + 2x_i \sum_{j \neq i} x_j - \frac{1}{N-1} \left(\sum_{j \neq i} x_j \right)^2 \right)}_{\alpha_i(\mathbf{x}, N, \rho_x, \sigma_x)} \right\} \right). \quad (3.5)$$

The ideal observer hence uses knowledge about the measurement correlations, ρ_x , in a decision.

We first confirm the intuitive observation that an ideal observer performs perfectly when measurement noise is highly correlated, $1 - \rho_x \ll 1$. In this case the exponential term in Eq. (3.5) is, to leading order in $1/(1 - \rho_x)$,

$$\alpha_i(\mathbf{x}, N, \rho_x, \sigma_x) \approx \exp \left[\frac{N-1}{2N\sigma_x^2(1-\rho_x)} (x_i - \bar{x}_i)^2 \right], \quad (3.6)$$

where $\bar{x}_i = 1/(N-1) \sum_{j \neq i} x_j$ is the sample mean of the measurements *excluding* the putative target, i . Hence, to make a decision, the ideal observer subtracts the mean of the $N-1$ measurements of putative distractors from that of the putative target. In Appedix B.1 we show that on “target absent” trials, $d_{\text{TD}}(\mathbf{x}) \rightarrow -\infty$, as $\rho_x \rightarrow 1$, and on target present trials, $d_{\text{TD}}(\mathbf{x}) \rightarrow \infty$, as $\rho_x \rightarrow 1$. Hence performance improves as measurement correlations increase. This can also be seen in Fig. 2B, as the overlap between the distributions $p(\mathbf{x}|T=0)$ and $p(\mathbf{x}|T=1)$ decreases with an increase in ρ_x .

When measurement correlations are absent, $\rho_x = 0$, an ideal observer performs perfectly only when measurement noise is vanishing. The exponential in Eq. (3.5) now equals

$$\begin{aligned} \alpha_i(\mathbf{x}, N, \rho_x, \sigma_x) &= \exp \left[-\frac{1}{2\sigma_x^2} \left(\frac{1}{N} \left(\sum_j x_j \right)^2 - \frac{1}{N-1} \left(\sum_{j \neq i} x_j \right)^2 \right) \right] \\ &= \exp \left[-\frac{1}{2\sigma_x^2} (N\bar{x}^2 - (N-1)\bar{x}_i^2) \right], \end{aligned} \quad (3.7)$$

where \bar{x} is the sample mean of all observations. The ideal observer therefore compares the sample mean over *all measurements*, \bar{x} , with the sample mean over all observations excluding the putative target, \bar{x}_i . Since measurement noise is uncorrelated, averaging over all measurements is beneficial. This is a very different strategy than when measurement noise is highly correlated (Eq. (3.6)), and the ideal observer compares a *single* putative target measurement, x_i , to the sample mean of the remaining target measurements. As shown in Appendix B.1 at intermediate values of measurement correlations, $0 < \rho_x < 1$, the ideal observer uses a mixture of these two strategies.

Intuitively, an increased number of distractors make it more difficult to detect the target. An analysis of the decision variable in the limit $N \rightarrow \infty$ shows that this is indeed the case (See Appendix B.3).

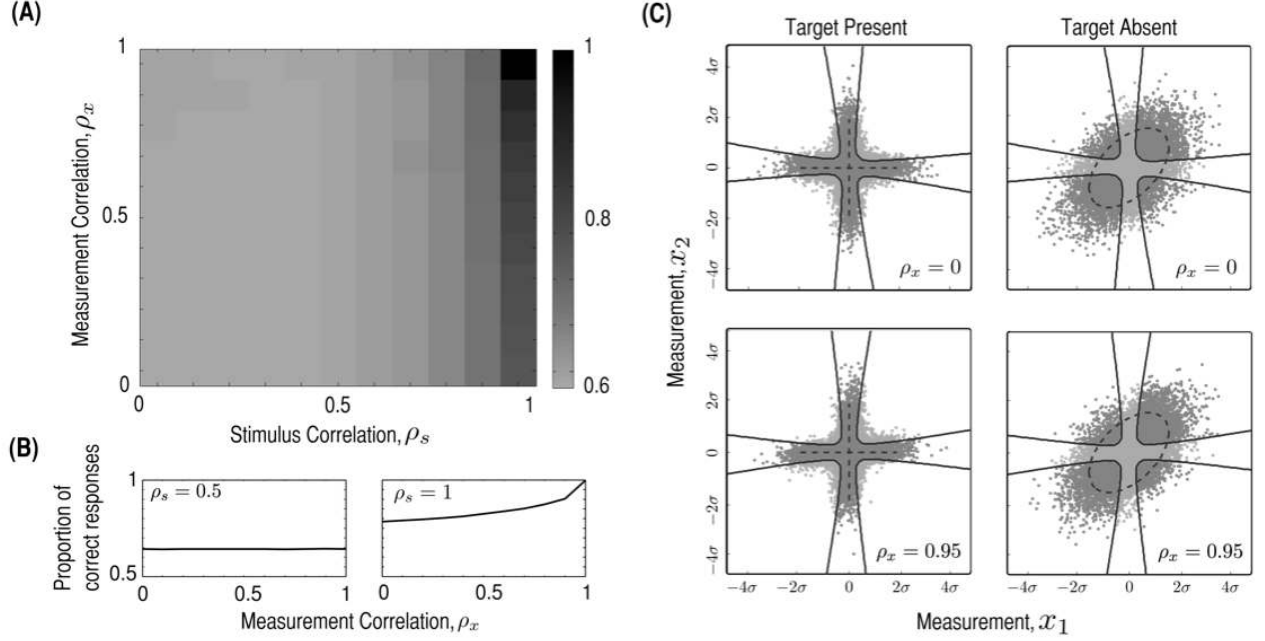


Figure 3: Performance of an optimal observer on a single target detection task with weak measurement noise, $\sigma_x^2 \ll \sigma_s^2$. **(A)** Proportion of correct responses as a function of stimulus correlation, ρ_s and measurement correlation, ρ_x , for $N = 4$ stimuli. **(B)** Proportion of correct responses as a function of measurement correlation, ρ_x , in the case of intermediate stimulus correlation, $\rho_s = 0.5$ (left) and strong correlation, $\rho_s = 1$ (right) for $N = 4$ stimuli. **(C)** Decision boundary, $d_{TD}(\mathbf{x}) = 0$ (black solid line) and measurement distributions on target present (left) and target absent (right) trials for $N = 2$ and $\rho_s = 0.5$. Here and henceforth dark gray dots correspond to measurements that result in a correct inference, and light gray dots correspond to measurements leading to an incorrect inference. The stimulus will result in a measurement that lies within the black dashed lines with probability 0.95. Other parameters used: $\sigma_s = 15$ and $\sigma_x = 4$.

Weak measurement noise, non-identical distractors, $\rho_s < 1$. Measurement correlations have little effect on performance when stimulus correlations are weaker (See Fig. 3A). Consider again $\rho_x \approx 1$, so that measurements are corrupted by adding a random, but nearly identical perturbation to the stimuli. An ideal observer uses the knowledge that all measurements are obtained by adding an approximately equal value to the stimulus. However, when stimulus correlations are weak, the target measurement is no longer an outlier. Correlations in measurement noise provide little help in this situation.

These observations are reflected in the structure of the decision boundaries ($d_{\text{TD}}(\mathbf{x}) = 0$), and the distributions of the measurements (See Fig. 3B). In the target absent (left column) and present trials (right column) the distributions of measurements, $p(\mathbf{x}|T)$, is shaped predominantly by variability in the stimulus. Measurement correlations have little effect on this shape, and the decision boundary therefore changes little with an increase in ρ_x . In contrast when $\rho_s \approx 1$, measurement correlations significantly impact the overlap between the distributions $p(\mathbf{x}|T = 1)$ and $p(\mathbf{x}|T = 0)$ as shown in Fig. 2B.

We can confirm this intuition about the role of measurement correlations by approximating the decision criterion when $\sigma_x^2 \ll \sigma_s^2$ and $\rho_s < 1$ (see details in Appendix B.4),

$$d_{\text{TD}}(\mathbf{x}) \approx \log \left(\frac{1}{N} \sqrt{\frac{\sigma_s^2(1 - \rho_s)(1 + (N - 1)\rho_s)}{\sigma_x^2(1 + (N - 2)\rho_s)}} \sum_{i=1}^N \exp \left\{ -\frac{x_i^2}{2\sigma_x^2} \right\} \right). \quad (3.8)$$

The strength of noise correlations, ρ_x , does not affect the decisions of an ideal observer at highest order in (σ_x^2/σ_s^2) . This explains the approximate independence of performance on ρ_x observed in Fig. 3B. In this case an ideal observer considers stimuli at each location separately, and weighs each measurement individually by its precision, $1/\sigma_x^2$ (Green and Swets, 1966; Palmer, 1999).

When the number of distractors becomes larger, Eq. (3.8) is no longer valid. The observer compares measurements of all stimuli to make a decision. We return to this point below.

Strong measurement noise, $\sigma_x^2 = \sigma_s^2$ Increasing measurement noise trivially degrades performance. However, in the limit of perfect stimulus and measurement correlations, an ideal observer still performs perfectly for the reasons described earlier.

Measurement correlations affect performance differently than in the case of weak measurement noise (See Fig. 4A,C). Even with uncorrelated stimuli, $\rho_s = 0$, performance increases slightly (approximately 5-6%) with ρ_x . Surprisingly, for intermediate values of stimulus correlations, *e.g.* $\rho_s = 0.5$, measurement correlations negatively impact performance. If measurement correlations are fixed at a high value, then the worst performance is observed at an intermediate value, $0 < \rho_s < 1$. The reason for this unexpected behavior is unclear, as Eq. (3.4) is difficult to analyze in this case.

Generally, when measurement noise is strong, measurement correlations will change the shape of the measurement distributions $p(\mathbf{x}|T = 0)$ and $p(\mathbf{x}|T = 1)$, and hence impact decisions and performance. Note that when measurement correlations increase, the region corresponding to $d_{\text{TD}}(\mathbf{x}) > 0$ is elongated along the diagonal to capture more of the mass of the distribution $p(\mathbf{x}|T = 1)$ (See Fig. 4C). However, when measurement noise is high, the interactions between measurement and stimulus correlations are intricate.

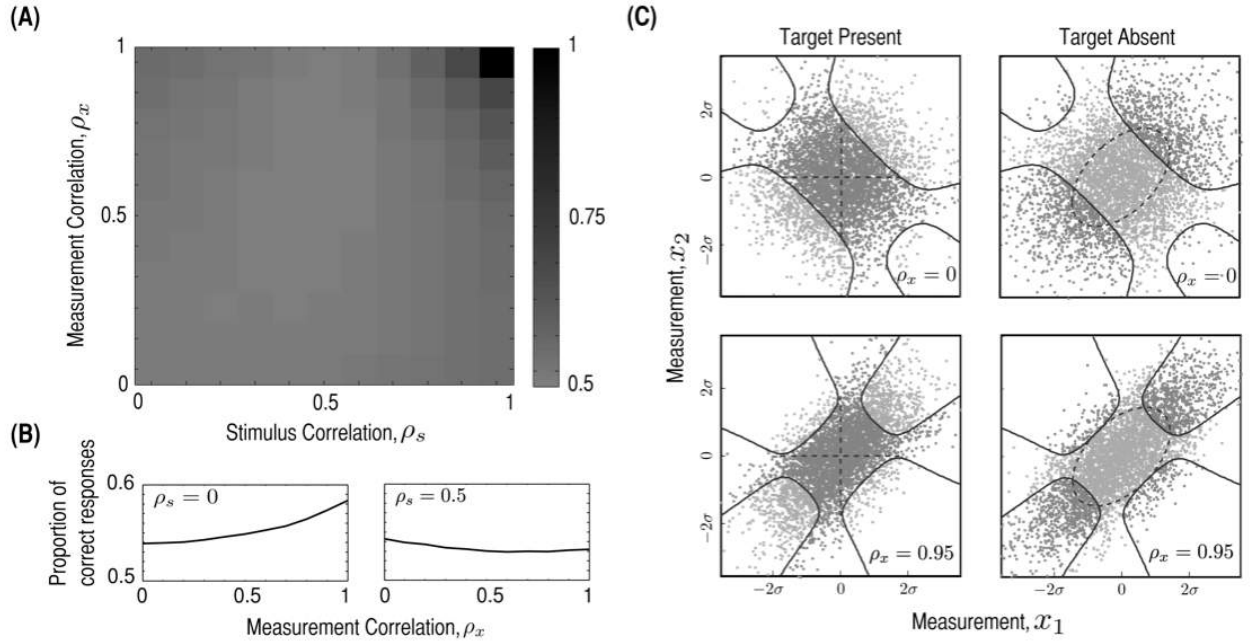


Figure 4: Performance of an optimal observer on a single target detection task with strong measurement noise, $\sigma_x^2 = \sigma_s^2$. **(A)** Proportion of correct responses as a function of ρ_s and ρ_x for $N = 4$ stimuli. **(B)** Performance as a function of measurement correlation, ρ_x , when $\rho_s = 0$ (left) and $\rho_s = 0.5$ (right) for $N = 4$ stimuli. **(C)** Decision boundary (black solid line) and distribution of measurements, \mathbf{x} on target present (left) and target absent (right) trials for $N = 2$ and $\rho_s = 0.5$. Other parameters used: $\sigma_s = \sigma_x = 15$.

3.2 Multiple targets, $n > 1$

In the present task when multiple targets are present, they are all identical and hence perfectly correlated. Thus, regardless of the value of ρ_s , on half the trials the stimuli will be strongly structured, and the density $p(\mathbf{s}|T = 1)$ concentrated on a low dimensional subspace. As a consequence, measurement correlations always impact performance.

Regardless of stimulus correlations, an ideal observer performs perfectly when $\rho_x = 1$ (See Fig. 5A). Even when $\rho_s < 1$, performance increases with ρ_x (see Fig. 5A). When $\rho_x = 1$, all target measurements are identical. Hence, an ideal observer performs perfectly by checking whether n of the measurements, x_i , are equal. We only analyze the case $\rho_s < 1$, since the case of perfectly correlated distractors is similar.

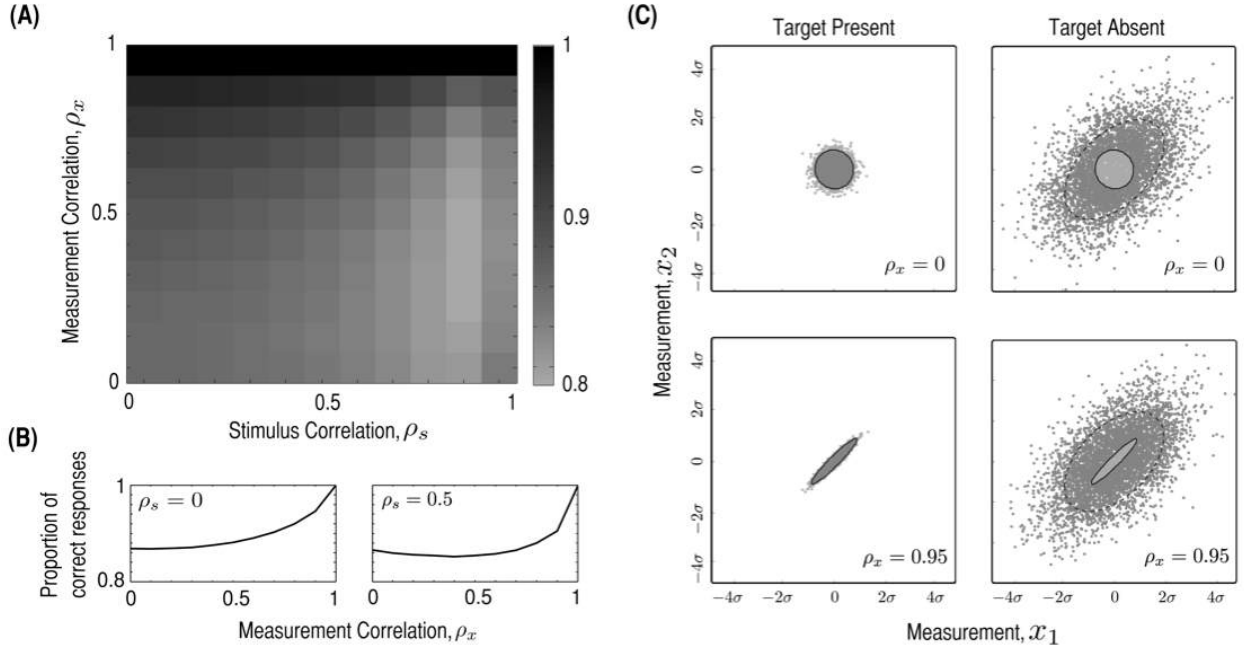


Figure 5: Performance of an optimal observer in a multiple target search task with weak measurement noise, $\sigma_x^2 \ll \sigma_s^2$. **(A)** Proportion of correct responses as a function of stimulus correlation, ρ_s , and measurement correlation, ρ_x , with $N = 4$ stimuli and $n = 3$ targets. **(B)** Proportion of correct responses as a function of ρ_x for $\rho_s = 0$ (left) and $\rho_s = 0.5$ (right) when $N = 4$ and $n = 3$. **(C)** Measurement distributions and decision boundary on target present (left) and target absent (right) trials for $\rho_s = 0.5$ and $N = n = 2$.

With weak measurement noise, Eq. (3.4) can be approximated as (see Appendix B.4):

$$d_{TD}(\mathbf{x}) \approx \log \left(\frac{1}{M} \sqrt{\frac{(1 - \rho_x)(1 + (N - 1)\rho_s)}{(1 + (N - n - 1)\rho_s)(1 + (n - 1)\rho_s)}} \left(\frac{\sigma_s^2(1 - \rho_s)}{\sigma_x^2(1 - \rho_x)} \right)^n \right. \\ \left. \times \sum_{L \in \mathcal{L}} \exp \left\{ -\frac{n}{2\sigma_x^2(1 - \rho_x)} \left(\frac{1}{n} \sum_{i \in L} x_i^2 - \frac{n\rho_x}{(1 + (n - 1)\rho_x)} \left(\frac{1}{n} \sum_{i \in L} x_i \right)^2 \right) \right\} \right). \quad (3.9)$$

An ideal observer takes into account measurement correlations for all values of ρ_s even when measurement noise is low. Stimulus correlations only appear in the prefactor, and are not used in the comparison of the measurements inside the exponential.

Interestingly, decisions in this case are based only on measurements of stimuli within the set of putative targets, L . In the absence of measurement correlations, a decision is based solely on the sample second moment of the n stimulus measurements *about the target characteristic*, $s_T = 0$, i.e. $1/n \sum_{i \in L} x_i^2$ (the underlined term in Eq. (3.9)). A low value of this sample moment indicates that L contains targets.

In the limit of $\rho_x \rightarrow 1$, the underlined term in Eq. (3.9) approaches the sample variance, $s_{i \in L}^2$, i.e. the sample second moment about the sample mean,

$$\frac{1}{n} \sum_{i \in L} x_i^2 - \frac{n\rho_x}{1 + \rho_x(n-1)} \left(\frac{1}{n} \sum_{i \in L} x_i \right)^2 \rightarrow \frac{1}{n} \sum_{i \in L} x_i^2 - \left(\frac{1}{n} \sum_{i \in L} x_i \right)^2 = s_{i \in L}^2. \quad (3.10)$$

If measurement correlations are strong, the measurements of a set of target stimuli will be approximately equal (regardless of ρ_s). The ideal observer makes use of this knowledge by comparing the value of putative targets in the set L . If the sample variance of the measurements $\{x_i\}_{i \in L}$ is small, then it is likely that L is a set of targets. When $\rho_x = 1$, an ideal observer performs perfectly (See Appendix B.5 for details).

When $0 < \rho_x < 1$, the underlined term in Eq. (3.9) shows that the ideal observer takes an intermediate strategy by computing a second moment about a point between the target characteristic, s_T , and the sample mean. Interestingly, the larger the number of targets, the larger the weight on the sample mean, since the prefactor $n\rho_x/(1 + (n-1)\rho_x)$ increases with n for fixed ρ_x .

These observations are reflected in the distributions shown in Fig. 5C. The distribution of measurements, $p(\mathbf{x}|T=1)$, move closer to the diagonal ($x_1 = x_2$) as $\rho_x \rightarrow 1$, and the overlap with the distribution of measurements, $p(\mathbf{x}|T=0)$ decreases. In higher dimensions, for N stimuli and n targets, the measurement distributions, $p(\mathbf{x}|T=1)$, is concentrated on the union of $(N-n+1)$ -dimensional subspaces when $\rho_x = 1$: The target measurements lie on a line, while the $N-n$ distractor measurements are distributed along the remaining directions.

To conclude, when there are multiple targets part of the stimulus set is always perfectly correlated. When measurement correlations are high, the observer checks whether the measurements are similar to each other to make a decision. When measurement correlations are low, the observer compares the measurements to the known target value. Measurement correlations can again decrease the overlap between the conditional distributions of measurements, and significantly impact decisions and performance. For finite N , decisions are based on the comparison of measurements within a putative set of stimuli, L . We show next that when N is large, this is no longer the case.

3.3 Larger number of targets and stimuli

If we assume a fixed proportion, K , of the stimuli consists of targets, so that $n = KN$, then Eq. (3.4) simplifies considerably in the limit of large N . If we let $c_x = \sigma_x^2(1 - \rho_x)$ and

$c_s = \sigma_s^2(1 - \rho_s)$, the exponential in Eq. (3.4) has the form, (See Appendix B.6)

$$\alpha_L(\mathbf{x}, N, c_x, c_s) \approx \exp \left(-\frac{1}{2} \left[\underbrace{\frac{NK}{c_x} s_{i \in L}^2}_I - \underbrace{\frac{N}{c_s + c_x} s^2}_{II} + \underbrace{\frac{N(1-K)}{c_s + c_x} s_{i \notin L}^2}_{III} \right] \right), \quad (3.11)$$

where $s_{i \in L}^2$, $s_{i \notin L}^2$, and s^2 are the sample variances of measurements from the putative target set, L , outside of the putative target set, and over all N measurements, respectively.

The different terms in this expression can be interpreted as earlier: Term I is the sample variance of measurements of the putative targets. If this variance is large, then the set L is unlikely to contain targets. Term II is the sample variance among all terms. If this term is large then all stimuli are dissimilar, and there is evidence that targets are present: For example, when distractors are correlated, and $c_s \ll 1$, then the sample variance of all stimulus measurements is small only in the absence of targets. Finally, term III is the sample variance among putative distractors. If distractors are correlated, this term will be small if L contains targets, and hence stimuli outside L are distractors. The sign of the three terms agrees with this interpretation: Terms I and III are negative, and term II is positive.

The main difference between the cases of large N , and the examples discussed previously is that an observer takes into account putative distractor measurements, *i.e.* measurements outside the putative target set L . An exception is the case when measurement correlations are much stronger than distractor correlations, $c_x \ll c_s$. In this case, the putative targets are more strongly structured, and hence only their measurements are used in a decision. When $c_s \ll 1$, or, equivalently, $\rho_s \approx 1$, and distractors are strongly correlated, all three terms in Eq. (3.11) are comparable. In this case, ideal observers base their decision on the similarity, as measured by sample variance, of both putative distractor and target measurements.

Importantly, the decision is made using distractor measurements, even when distractors are not perfectly correlated. Fig 6 shows that intermediate distractor correlations have an increasingly impact decisions with an increase in distractor number. Indeed, the higher the fraction of distractors, $(1 - K)$, the more weight is assigned to their sample variance (term III). This is unlike the case of small N , where distractor measurements are used only when they are perfectly correlated.

4 Discussion

We have shown that in a simple task the statistical structure of the stimulus as well as that of noise in perceptual measurements determine the strategy and performance of an ideal observer. Correlations in measurement noise can significantly impact performance, particularly when stimulus correlations are high: When the distribution of stimuli conditioned on the parameter of interest is concentrated in a small volume of stimulus space, the statistical structure of measurement noise can be of particular importance (Mazyar et al., 2012, 2013; Bhardwaj et al., 2015).

The impact of noise correlations on the inference of a parameter from neural responses has been studied in detail (Averbeck et al., 2006; Averbeck, 2009; Latham and Nirenberg,

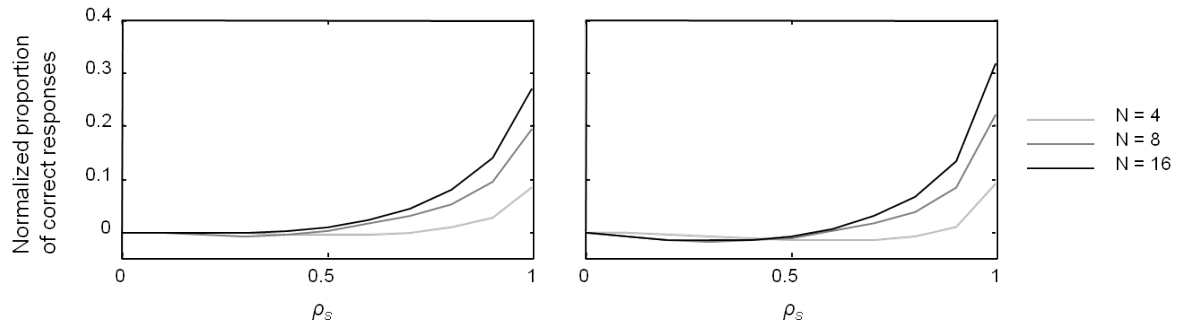


Figure 6: Normalized performance of an optimal observer with respect to $\rho_s = 0$ as a function of stimulus correlation, ρ_s , for different values of N in case of (A) $\rho_x = 0$ and (B) $\rho_x = 0.5$. Intermediate correlations between distractor measurements become increasingly important as the number of distractors increases from four to sixteen. Other parameters used: $\sigma_s = 15$, $\sigma_x = 4$, and $n = 2$.

2005; Perkel et al., 1967; Schneidman et al., 2003; Sompolinsky et al., 2001). Frequently the parameter of interest was identified with the stimulus, and both were univariate. The estimation of the orientation of a bar in the receptive field of a population of neurons has been a canonical example.

Reality is far more complex. Stimuli, such as a natural visual or auditory scene, are high dimensional and highly structured. Moreover, only some of the parameters are typically relevant. Intuitively, if noise perturbs measurements along relevant direction, *i.e.* along the directions of the parameters of interest, then estimates will be corrupted. Perturbations along irrelevant directions in parameter space have little effect (Moreno-Bote et al., 2014). Measurement correlations can channel noise into irrelevant directions, without decreasing overall noise magnitude, and thus improve parameter inference.

This is difficult to study using general theoretical models without putting some constraints on the structure of measurement noise. We therefore considered a relatively simple, analytically tractable example where both measurement and stimulus structure are characterized by a small number of parameters. We have used a similar setup to examine decision making in controlled search experiments (Mazyar et al., 2012, 2013; Bhardwaj et al., 2015).

We assumed that measurement noise and measurement correlations can be varied independently. This is not realistic. For instance, it is known that changes in the mean, variability and covariability of neural responses can be tightly linked (Cohen and Kohn, 2011; de la Rocha et al., 2007; Rosenbaum and Josić, 2011). It is thus likely that the statistics of measurement noise also change in concert. However, at present this relationship has not been well characterized.

More importantly, noise from the periphery of the nervous system will limit the performance of any observer. It is therefore not possible that a simple change in measurement correlations can lead to perfect performance (Moreno-Bote et al., 2014). To address this question it would be necessary to provide a more accurate model of both the noise correlations in a recurrent network encoding information about the stimuli (Beck et al., 2011), as well as the resulting measurement correlations. This is beyond the scope of the present study.

We also made strong assumptions about the structure of measurement and stimulus correlations. We chose to restrict our analysis to positive correlations. The reason is that the requirement that a covariance matrix is positive definite implies restrictions on the range of allowable negative measurement and stimulus correlations (Horn and Johnson, 2012). These restrictions depend on the number of stimuli, N , and complicate the analysis. To make the model tractable, we also assumed that all off-diagonal elements in the stimulus and measurement noise covariance matrices are identical. While we did not examine it here, heterogeneity in the correlation structure can strongly affect parameter inference (Shamir and Sompolinsky, 2006; Chelaru and Dragoi, 2008; Berens et al., 2011).

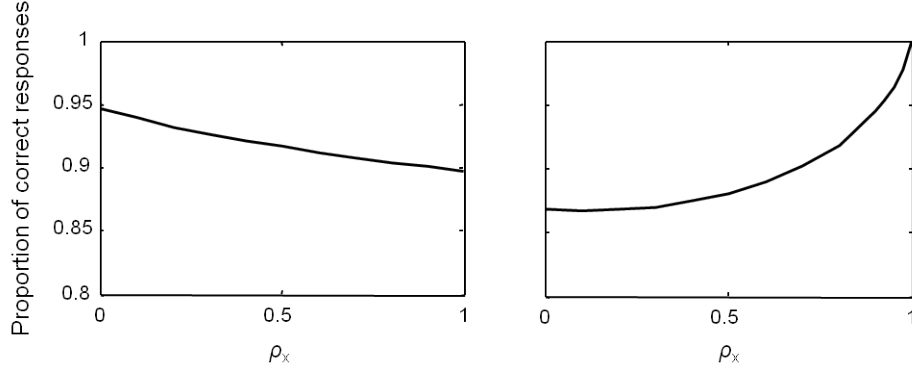


Figure 7: Performance comparison of an optimal observer as a function of measurement correlations in **(A)** a mean left/right discrimination task with $N = 4$ stimuli and **(B)** a target detection task with $n = 3$ targets. Other parameters used: $\sigma_s = 15$, $\sigma_x = 4$, and $\rho_s = 0.5$.

To end, we provide another illustration of the fact that measurement correlations can affect the performance of an ideal observer in different ways depending on the task: Suppose an observer is presented with N oriented stimuli, such as Gabor patches. The stimuli and measurements follow the same Gaussian distributions introduced earlier in this study. The observer is asked to perform one of the following two tasks: 1) Report whether the mean orientation of the stimuli is to the left or right of vertical; 2) Report whether a vertically oriented target is present or absent. In this case, a subset of the stimuli has vertical orientation on half the trials.

The first task is a discrimination task, and the observer needs to integrate information from different sources. When measurement correlations are high, it is more difficult to average out the noise between the stimulus measurements (Sompolinsky et al., 2001; Zohary et al., 1994). The estimate of the average orientation is therefore degraded and performance decreases with an increase in measurement correlations (see Fig. 7A and Appendix C). The second is a detection task that requires extracting information that is buried in a sea of distractors. As discussed above, in this case measurement correlations can increase performance if there is more than one target, or if the distractors are strongly correlated (see Fig. 7B).

In this example the stimuli and the measurements have the same statistical structure on target absent trials for the two tasks. However, the parameter of interest differs: In the first task the observer needs to estimate the average stimulus orientation, and in the second

determine whether a target is present. The distributions of measurements conditioned on these parameters are therefore also different, and are differently affected by measurement noise.

The question of how measurement correlations impact decision making and performance does not have a simple answer (Hu et al., 2014). Correlations in measurement noise can have a pronounced effect when the stimuli themselves are highly correlated, *i.e.* when they occupy a small volume in stimulus space. We have illustrated how in this case measurement correlations can help in separating the distribution of measurements conditioned on a parameter of interest. Similar considerations will be important whenever we try to understand how information can be extracted from the collective responses of neural populations to high dimensional, and highly structured stimuli.

5 Acknowledgment

K.J. was supported by NSF award DMS-1122094. W.J.M. was supported by award number R01EY020958 from the National Eye Institute and award number W911NF-12-1-0262 from the Army Research Office.

Appendices

A Derivation of Eqs. (3.3) and (3.4)

Here we present the details of some of the calculations leading to the results presented in the main text. The computations rely on the assumption of Gaussianity. We will therefore make repeated use of the fact that the density $\mathcal{N}(\mathbf{x}; \boldsymbol{\mu}, \boldsymbol{\Sigma})$ of the normal distribution with mean $\boldsymbol{\mu}$, and covariance $\boldsymbol{\Sigma}$ is

$$\mathcal{N}(\mathbf{x}; \boldsymbol{\mu}, \boldsymbol{\Sigma}) = \frac{1}{\sqrt{(2\pi)^N |\boldsymbol{\Sigma}|}} \exp \left(-\frac{1}{2} (\mathbf{x} - \boldsymbol{\mu})^T \boldsymbol{\Sigma}^{-1} (\mathbf{x} - \boldsymbol{\mu}) \right), \quad (\text{A.1})$$

where $|\boldsymbol{\Sigma}|$ denotes the determinant of the matrix $\boldsymbol{\Sigma}$.

Let $M = \binom{N}{n}$ denote the cardinality of the set \mathcal{L} of all possible sets L . We compute $p(\mathbf{x}|T=1)$ in Eq. (3.1) by marginalizing over \mathbf{s} ,

$$p(\mathbf{x}|T=1) = \int p(\mathbf{x}|\mathbf{s})p(\mathbf{s}|T=1)d\mathbf{s}.$$

We note that

$$p(\mathbf{s}|T=1) = \sum_{L \in \mathcal{L}} p(\mathbf{s}|T=1, L)p(L) = \frac{1}{M} \sum_{L \in \mathcal{L}} p(\mathbf{s}|T=1, L).$$

Therefore,

$$\begin{aligned}
p(\mathbf{x}|T=1) &= \frac{1}{M} \int p(\mathbf{x}|\mathbf{s}) \sum_{L \in \mathcal{L}} p(\mathbf{s}|T=1, L) d\mathbf{s} \\
&= \frac{1}{M} \sum_{L \in \mathcal{L}} \int p(\mathbf{x}|\mathbf{s}) p(\mathbf{s}|T=1, L) d\mathbf{s} \\
&= \frac{1}{M} \lim_{\eta \rightarrow 0} \sum_{L \in \mathcal{L}} \int \mathcal{N}(\mathbf{x}; \mathbf{s}, \Sigma_{\mathbf{x}}) \mathcal{N}(\mathbf{s}; \mathbf{0}_N, \Sigma_{\mathbf{s}, L}^{\eta}) d\mathbf{s} \\
&= \frac{1}{M} \sum_{L \in \mathcal{L}} \mathcal{N}(\mathbf{x}; \mathbf{0}_N, \mathbf{C}_L),
\end{aligned}$$

Similarly,

$$\begin{aligned}
p(\mathbf{x}|T=0) &= \int p(\mathbf{x}|\mathbf{s}) p(\mathbf{s}|T=0) d\mathbf{s} \\
&= \int \mathcal{N}(\mathbf{x}; \mathbf{s}, \Sigma_{\mathbf{x}}) \mathcal{N}(\mathbf{s}; \mathbf{0}_N, \Sigma_{\mathbf{s}}) d\mathbf{s} \\
&= \mathcal{N}(\mathbf{x}; \mathbf{0}_N, \mathbf{C}),
\end{aligned}$$

where $\mathbf{C}_L = \Sigma_{\mathbf{x}} + \Sigma_{\mathbf{s}, L}^0$ and $\mathbf{C} = \Sigma_{\mathbf{x}} + \Sigma_{\mathbf{s}}$. We therefore obtain

$$\begin{aligned}
d_{\text{TD}}(\mathbf{x}) &= \log \frac{p(\mathbf{x}|T=1)}{p(\mathbf{x}|T=0)} = \log \left(\frac{1}{M} \sum_{L \in \mathcal{L}} \frac{\mathcal{N}(\mathbf{x}; \mathbf{0}_N, \mathbf{C}_L)}{\mathcal{N}(\mathbf{x}; \mathbf{0}_N, \mathbf{C})} \right) \\
&= \log \left(\frac{1}{M} \sqrt{\frac{|\mathbf{C}|}{|\mathbf{C}_L|}} \sum_{L \in \mathcal{L}} \exp \left(-\frac{1}{2} \mathbf{x}^T (\mathbf{C}_L^{-1} - \mathbf{C}^{-1}) \mathbf{x} \right) \right). \tag{A.2}
\end{aligned}$$

We note that the determinant of \mathbf{C}_L does not depend on the set L since all matrices \mathbf{C}_L can be obtained from each other by permuting appropriate rows and columns.

In the case variances and covariances are equal, we can invert \mathbf{C}_L and \mathbf{C} . In general, matrix \mathbf{C}_L has the following form,

$$(\mathbf{C}_L)_{i,j} = \begin{cases} \sigma_x^2, & \text{if } i = j \in L, \\ \sigma_s^2 + \sigma_x^2, & \text{if } i = j \notin L, \\ \rho_x \sigma_x^2, & \text{if } i \neq j, \text{ and } i \text{ or } j \in L, \\ \rho_s \sigma_s^2 + \rho_x \sigma_x^2, & \text{if } i \neq j, \text{ and } i, j \notin L, \end{cases}$$

We will use the Sherman-Morrison-Woodbury formula (Meyer, 2000),

$$(A + UEV)^{-1} = A^{-1} - A^{-1}U(E^{-1} + VA^{-1}U)^{-1}VA^{-1}, \tag{A.3}$$

to obtain the inverses of \mathbf{C}_L and \mathbf{C} . To do so we first rewrite \mathbf{C}_L as $A_L + U_LEV_L$: When $L = \{1, 2, \dots, n\}$ (targets placed at the first n out of N possible locations), we have

$$\begin{aligned}
A_L &= \begin{bmatrix} (\sigma_x^2 - b)I_n & 0_{n \times (N-n)} \\ 0_{(N-n) \times n} & (\sigma_s^2 + \sigma_x^2 - a)I_{(N-n)} \end{bmatrix}_{(N \times N)}, & U_L &= \begin{bmatrix} b & \cdots & b & a & \cdots & a \\ b & \cdots & \cdots & \cdots & \cdots & b \end{bmatrix}_{(N \times 2)}^T, \\
V_L &= \begin{bmatrix} 0 & \cdots & 0 & 1 & \cdots & 1 \\ 1 & \cdots & 1 & 0 & \cdots & 0 \end{bmatrix}_{(2 \times N)}, & \text{and} & E &= \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}_{(2 \times 2)},
\end{aligned}$$

where $a = \rho_s \sigma_s^2 + \rho_x \sigma_x^2$, and $b = \rho_x \sigma_x^2$.

Using Eq. (A.3) we obtain

$$(\mathbf{C}_L^{-1})_{i,j} = \begin{cases} v_L - \frac{bv_L^2 g_L}{\gamma_L}, & \text{if } i = j \in L, \\ v - \frac{v^2 f_L}{\gamma_L}, & \text{if } i = j \notin L, \\ -\frac{bv_L^2 g_L}{\gamma_L}, & \text{if } i \neq j, \text{ and } i, j \in L, \\ -\frac{v^2 f_L}{\gamma_L}, & \text{if } i \neq j, \text{ and } i, j \notin L, \\ -\frac{bv_L v_L}{\gamma_L}, & \text{if } i \neq j, i \in L, j \notin L \text{ or } i \neq j, i \notin L, j \in L, \end{cases}$$

where

$$\begin{aligned} v &= \frac{1}{\sigma_s^2(1 - \rho_s) + \sigma_x^2(1 - \rho_x)}, & v_L &= \frac{1}{\sigma_x^2(1 - \rho_x)}, & f_L &= a + n\rho_s \sigma_s^2 \rho_x \sigma_x^2 v_L \\ g_L &= 1 + \rho_s \sigma_s^2 (N - n)v, & \text{and } \gamma_L &= 1 + a(N - n)v + n\rho_x \sigma_x^2 v_L g_L. \end{aligned} \quad (\text{A.4})$$

Using the Matrix Determinant Lemma (Harville, 1998), we can obtain the determinant of \mathbf{C}_L

$$\det(\mathbf{C}_L) = \frac{\gamma_L}{v_L^n v^{N-n}}.$$

Similarly, we compute the inverse and determinant of matrix \mathbf{C} ,

$$\mathbf{C}^{-1} = \begin{bmatrix} v - \beta v^2 & -\beta v^2 & \cdots & -\beta v^2 \\ -\beta v^2 & v - \beta v^2 & \cdots & -\beta v^2 \\ \vdots & & \ddots & \\ -\beta v^2 & -\beta v^2 & \cdots & v - \beta v^2 \end{bmatrix},$$

where

$$\beta = \frac{a}{1 + aNv}, \quad (\text{A.5})$$

and

$$\det(\mathbf{C}) = \frac{1 + aNv}{v^N}.$$

The prefactor in Eq. (A.2), is therefore

$$\sqrt{\frac{|\mathbf{C}|}{|\mathbf{C}_L|}} = \sqrt{\frac{1 + aNv}{\gamma_L} \left(\frac{v_L}{v}\right)^n},$$

and we can compute

$$\begin{aligned} \mathbf{x}^T \mathbf{C}^{-1} \mathbf{x} &= (v - \beta v^2) \sum_{i=1}^N x_i^2 - \beta v^2 \sum_{i \neq j}^N x_i x_j, \\ \mathbf{x}^T \mathbf{C}_L^{-1} \mathbf{x} &= \left(v_L - \frac{1}{\gamma_L} b v_L^2 g_L\right) \sum_{i \in L} x_i^2 + \left(v - \frac{1}{\gamma_L} v^2 f_L\right) \sum_{i \notin L} x_i^2 - \frac{1}{\gamma_L} b v_L^2 g_L \sum_{\substack{i, j \in L \\ i \neq j}} x_i x_j \\ &\quad - \frac{2}{\gamma_L} b v v_L \sum_{\substack{i \in L \\ j \notin L}} x_i x_j - \frac{1}{\gamma_L} v^2 f_L \sum_{\substack{i, j \notin L \\ i \neq j}} x_i x_j. \end{aligned}$$

A slight rearrangement of the terms therefore shows that when variances and covariances are equal, Eq. (A.2) is equivalent to

$$d_{\text{TD}}(\mathbf{x}) = \log \left(\frac{1}{M} \sqrt{\frac{1 + aNv}{\gamma_L}} \left(\frac{v_L}{v} \right)^n \sum_{L \in \mathcal{L}} \exp \left\{ -\frac{1}{2} \left(\sigma_s^2(1 - \rho_s)v_L v \sum_{i \in L} x_i^2 \right. \right. \right. \\ \left. \left. \left. + \left(\beta v^2 - \frac{v_L^2 b g_L}{\gamma_L} \right) \sum_{i,j \in L} x_i x_j + 2 \left(\beta v^2 - \frac{v_L v b}{\gamma_L} \right) \sum_{i \in L, j \notin L} x_i x_j + \left(\beta v^2 - \frac{f_L v^2}{\gamma_L} \right) \sum_{i,j \notin L} x_i x_j \right) \right\} \right).$$

B Asymptotic analysis of Eq. (3.4)

Here we present some asymptotic results for the decision variable $d_{\text{TD}}(\mathbf{x})$ given in Eq. (3.4). The main results are obtained for small measurement noise, σ_x^2 . Equivalent results can be obtained for large external variability, σ_s^2 .

B.1 Small measurement noise and identical distractors, $\rho_s = 1$

We first concentrate on the case $n = 1$. The exponential terms in Eq. (3.4) simplify to the following:

$$\begin{aligned} \sigma_s^2(1 - \rho_s)v_L v &= 0, \\ \beta v^2 - \frac{\rho_x \sigma_x^2 v_L^2 g_L}{\gamma_L} &= \frac{\sigma_s^2 + \rho_x \sigma_x^2}{\sigma_x^2(1 - \rho_x)[N\sigma_s^2 + \sigma_x^2(1 + (N - 1)\rho_x)]} \\ &\quad - \frac{\rho_x[\sigma_s^2(N - 1) + \sigma_x^2(1 - \rho_x)]}{\sigma_x^2(1 - \rho_x)[\sigma_s^2(N - 1) + \sigma_x^2(1 - \rho_x)(1 + (N - 1)\rho_x)]} \\ &= \frac{1 - N\rho_x}{N\sigma_x^2(1 - \rho_x)} + \mathcal{O}(1), \\ \beta v^2 - \frac{\rho_x \sigma_x^2 v_L v}{\gamma_L} &= \frac{\sigma_s^2 + \sigma_x^2 \rho_x}{\sigma_x^2(1 - \rho_x)[N\sigma_s^2 + \sigma_x^2(1 + (N - 1)\rho_x)]} - \frac{\rho_x}{\sigma_s^2(N - 1) + \sigma_x^2(1 - \rho_x)(1 + (N - 1)\rho_x)} \\ &= \frac{1}{N\sigma_x^2(1 - \rho_x)} + \mathcal{O}(1), \\ \beta v^2 - \frac{v^2 f_L}{\gamma_L} &= \frac{\sigma_s^2 + \sigma_x^2 \rho_x}{\sigma_x^2(1 - \rho_x)[N\sigma_s^2 + \sigma_x^2(1 + (N - 1)\rho_x)]} \\ &\quad - \frac{\sigma_s^2 + \rho_x \sigma_x^2(1 - \rho_x)}{\sigma_x^2(1 - \rho_x)[\sigma_s^2(N - 1) + \sigma_x^2(1 - \rho_x)(1 + (N - 1)\rho_x)]} \\ &= -\frac{1}{N(N - 1)\sigma_x^2(1 - \rho_x)} + \mathcal{O}(1). \end{aligned}$$

And the leading determinant term becomes:

$$\begin{aligned} \sqrt{\frac{1 + aNv}{\gamma_L} \frac{v_L}{v}} &= \sqrt{\frac{(1 - \rho_x)[N\sigma_s^2 + \sigma_x^2(1 + (N - 1)\rho_x)]}{\sigma_s^2(N - 1) + \sigma_x^2(1 - \rho_x)(1 + (N - 1)\rho_x)}} \\ &= \sqrt{\frac{N(1 - \rho_x)}{N - 1}} + \mathcal{O}(\sigma_x^2) \end{aligned}$$

Therefore, the decision variable becomes approximately,

$$d_{\text{TD}}(\mathbf{x}) \approx \log \left(\frac{1}{N} \sqrt{\frac{N(1-\rho_x)}{N-1}} \sum_{i=1}^N \exp \left\{ \frac{-1}{2N\sigma_x^2(1-\rho_x)} \left((1-N\rho_x)x_i^2 + 2x_i \sum_{j \neq i} x_j - \frac{1}{N-1} \left(\sum_{j \neq i} x_j \right)^2 \right) \right\} \right).$$

After rearranging terms, this can be rewritten as

$$d_{\text{TD}}(\mathbf{x}) \approx \log \left(\frac{1}{N} \sqrt{\frac{N(1-\rho_x)}{N-1}} \sum_{i=1}^N \exp \left[\rho_x \frac{N-1}{2N\sigma_x^2(1-\rho_x)} (x_i - \bar{x}_i)^2 - \frac{1}{2\sigma_x^2} (N\bar{x}^2 - (N-1)\bar{x}_i^2) \right] \right), \quad (\text{B.1})$$

where \bar{x} is the sample mean of all measurements, and where \bar{x}_i is the sample mean of the measurements *excluding* the putative target, i . In the limiting cases $\rho_x = 0$ and $(1-\rho_x) \ll 1$, we obtain the exponents given in Eq. (3.6) and Eq. (3.7) discussed in the text.

B.2 Perfect performance when $\rho_x = 1$

We show that when $\rho_s = 1$, an ideal observer performs perfectly in the limit of identical measurement noise. For a fixed number of stimuli, N , on “target absent” trials, $x_i - (N-1)^{-1} \sum_{j \neq i} x_j = O(\sqrt{\epsilon})$, and hence $\alpha(\mathbf{x}, N, \rho_x, \sigma_x) = O(1)$. On the other hand the prefactor, $P(N, \rho_x) = O(\sqrt{\epsilon})$, and hence $d_{\text{TD}}(\mathbf{x}) \rightarrow -\infty$, as $\epsilon \rightarrow 0$, *i.e.* as $\rho_x \rightarrow 1$. On “target present” trials, when stimulus i is the target, then $x_i - (N-1)^{-1} \sum_{j \neq i} x_j = O(1)$, and $\alpha_i(\mathbf{x}, N, \rho_x, \sigma_x) = O(1/\epsilon)$. In this case the prefactor is still $P(N, \rho_x) = O(\sqrt{\epsilon})$, and the exponential term dominates. A similar argument works for the summands for which i is not a target.

B.3 Single target with increasing number of distractors

We still work under the assumption that measurement noise is relatively weak, so that we can use Eq. (B.1). Note that on “target absent” trials, $\bar{x} = s + O(\sigma_x^2/\sqrt{N})$, where s is the true value of the (identical) distractors. We also have $\bar{x}_i = s + O(\sigma_x^2/\sqrt{N-1})$. Hence, the first term in the exponential of Eq. (B.1) is $O(1)$, while the second term is $O(\sqrt{N})$. A similar argument holds in “target present” trials.

On target absent trials

$$-\frac{1}{2\sigma_x^2} (N\bar{x}^2 - (N-1)\bar{x}_i^2) = \exp \left[-\frac{1}{2\sigma_x^2} s^2 + O(\sqrt{N}\sigma_x) \right] \quad \text{for all } i,$$

to leading order in N . We abuse notation slightly and only use order notation on the terms that include measurement noise. As stimuli become more dissimilar to the target, *i.e.* as s^2 increases, α_i decreases exponentially, $d_{\text{TD}}(\mathbf{x})$ becomes more negative, and it is hence easier to

infer that a target is absent. However, the $O(\sqrt{N}\sigma_x)$ terms can be both positive and negative. Thus performance decreases with the number of stimuli. Similarly we can see that when a target is present

$$\alpha_i(\mathbf{x}, N, \sigma_x^2) = \exp \left[\frac{1}{2\sigma_x^2} \frac{N-1}{N} s^2 + O(\sqrt{N}\sigma_x) \right] \quad \text{when } i \text{ is the target,} \quad (\text{B.2})$$

$$\alpha_i(\mathbf{x}, N, \rho_x) = \exp \left[-\frac{1}{2\sigma_x^2} \frac{1+N-N^2}{N-N^2} s^2 + O(\sqrt{N}\sigma_x) \right] \quad \text{when } i \text{ is not a target,} \quad (\text{B.3})$$

again to leading order in N . As measurement noise decreases, or s^2 increases, the first term given in Eq. (B.2) diverges exponentially, and the terms given in Eq. (B.3) approach 0 exponentially. As a result $d_{\text{TD}}(\mathbf{x})$ increases. However, the $O(\sqrt{N}\sigma_x)$ noise term increases with N , and an increase in the number of stimuli again decreases performance.

If $(1 - \rho_x) \ll 1/N$, *i.e.* measurement noise is strongly correlated, the first term in the exponential of Eq. (B.1) dominates. Thus when correlations increase faster than the inverse of the number of distractors, performance increases with the number of distractors.

B.4 Weak external structure, $\rho_s < 1$, arbitrary number of targets

We approximate each term in the exponential of Eq. (3.4) assuming $\sigma_x^2 \ll 1$:

$$\begin{aligned} \sigma_s^2(1 - \rho_s)v_L v &= \frac{\sigma_s^2(1 - \rho_s)}{\sigma_x^2(1 - \rho_x)[\sigma_s^2(1 - \rho_s) + \sigma_x^2(1 - \rho_x)]} \\ &= \frac{1}{\sigma_x^2(1 - \rho_x)} + \mathcal{O}(1), \\ \beta v^2 - \frac{\rho_x \sigma_x^2 v_L^2 g_L}{\gamma_L} &= \frac{\rho_s \sigma_s^2 + \rho_x \sigma_x^2}{[\sigma_s^2(1 - \rho_s) + \sigma_x^2(1 - \rho_x)][\sigma_s^2(1 + (N-1)\rho_s) + \sigma_x^2(1 + (N-1)\rho_x)]} \\ &\quad - \frac{\rho_x[\sigma_s^2(1 + (N-n-1)\rho_s) + \sigma_x^2(1 - \rho_x)]}{\sigma_x^2(1 - \rho_x)[\sigma_s^2(1 + (n-1)\rho_x)(1 + (N-n-1)\rho_s) + \sigma_x^2(1 - \rho_x)(1 + (N-1)\rho_x)]} \\ &= -\frac{\rho_x}{\sigma_x^2(1 - \rho_x)(1 + (n-1)\rho_x)} + \mathcal{O}(1), \\ \beta v^2 - \frac{\rho_x \sigma_x^2 v_L v}{\gamma_L} &= \frac{\rho_s \sigma_s^2 + \rho_x \sigma_x^2}{[\sigma_s^2(1 - \rho_s) + \sigma_x^2(1 - \rho_x)][\sigma_s^2(1 + (N-1)\rho_s) + \sigma_x^2(1 + (N-1)\rho_x)]} \\ &\quad - \frac{\rho_x}{[\sigma_s^2(1 + (N-n-1)\rho_s)(1 + (n-1)\rho_x) + \sigma_x^2(1 - \rho_x)(1 + (N-1)\rho_x)]} \\ &= \mathcal{O}(1), \end{aligned}$$

and

$$\begin{aligned} \beta v^2 - \frac{v^2 f_L}{\gamma_L} &= \frac{\rho_s \sigma_s^2 + \rho_x \sigma_x^2}{[\sigma_s^2(1 - \rho_s) + \sigma_x^2(1 - \rho_x)][\sigma_s^2(1 + (N-1)\rho_s) + \sigma_x^2(1 + (N-1)\rho_x)]} \\ &\quad - \frac{\rho_s \sigma_s^2(1 + (n-1)\rho_x) + \rho_x \sigma_x^2(1 - \rho_x)}{[\sigma_s^2(1 - \rho_s) + \sigma_x^2(1 - \rho_x)][\sigma_s^2(1 + (N-n-1)\rho_s)(1 + (n-1)\rho_x) + \sigma_x^2(1 - \rho_x)(1 + (N-1)\rho_x)]} \\ &= \mathcal{O}(1) \end{aligned}$$

We also approximate the leading coefficient of the exponential term in Eq. (3.4) as:

$$\begin{aligned}
& \sqrt{\frac{1 + (\rho_s \sigma_s^2 + \rho_x \sigma_x^2) N v}{\gamma_L}} \left(\frac{v_L}{v} \right)^n = \\
& \sqrt{\frac{(1 - \rho_x) [\sigma_s^2 (1 + (N - 1) \rho_s) + \sigma_x^2 (1 + (N - 1) \rho_x)]}{[\sigma_s^2 (1 + (N - n - 1) \rho_s) (1 + (n - 1) \rho_x) + \sigma_x^2 (1 - \rho_x) (1 + (N - 1) \rho_x)]}} \left(\frac{\sigma_s^2 (1 - \rho_s) + \sigma_x^2 (1 - \rho_x)}{\sigma_x^2 (1 - \rho_x)} \right)^n \\
& = \sqrt{\frac{(1 - \rho_x) (1 + (N - 1) \rho_s)}{(1 + (N - n - 1) \rho_s) (1 + (n - 1) \rho_x)}} \left(\frac{\rho_s (1 - \rho_s)}{\sigma_x^2 (1 - \rho_x)} \right)^n + \mathcal{O}(1).
\end{aligned}$$

Combining above terms, Eq. (3.4) reduces to the following expression under the assumption of $\sigma_x^2 \ll \sigma_s^2, \rho_s < 1$,

$$\begin{aligned}
d_{\text{TD}}(\mathbf{x}) \approx & \log \left(\frac{1}{M} \sqrt{\frac{(1 - \rho_x) (1 + (N - 1) \rho_s)}{(1 + (N - n - 1) \rho_s) (1 + (n - 1) \rho_x)}} \left(\frac{\sigma_s^2 (1 - \rho_s)}{\sigma_x^2 (1 - \rho_x)} \right)^n \right. \\
& \times \sum_{L \in \mathcal{L}} \exp \left\{ -\frac{1}{2\sigma_x^2 (1 - \rho_x)} \left(\sum_{i \in L} x_i^2 - \frac{\rho_x}{1 + (n - 1) \rho_x} \sum_{i, j \in L} x_i x_j \right) \right\} \Bigg).
\end{aligned}$$

Special case: $n = 1$ In case of a single target, set L has only one element and $\mathcal{L} = \{1, 2, \dots, N\}$. In this case, Eq. (3.9) reduces to a much simpler expression

$$d_{\text{TD}}(\mathbf{x}) \approx \log \left(\frac{1}{N} \sqrt{\frac{\sigma_s^2 (1 - \rho_s) (1 + (N - 1) \rho_s)}{\sigma_x^2 (1 + (N - 2) \rho_s)}} \sum_{i=1}^N \exp \left\{ -\frac{x_i^2}{2\sigma_x^2} \right\} \right).$$

This expression is independent of ρ_x . Hence, the decision boundary, and the performance of an ideal observer is unaffected by measurement correlations.

B.5 Near perfect performance with $n > 1$, and $\rho_x \approx 1$

We first assume that $T = 1$. From Eq. (3.10), if L_T is the set of targets, then this expression is approximately zero, and the exponential is approximately unity. When L is a set not consisting of all targets, then the expression in Eq. (3.10) has expectation greater than zero. Then

$$\begin{aligned}
& \sum_{L \in \mathcal{L}} \exp \left\{ -\frac{n}{2\sigma_x^2 (1 - \rho_x)} \left(\frac{1}{n} \sum_{i \in L} x_i^2 - \left(\frac{1}{n} \sum_{i \in L} x_i \right)^2 \right) \right\} = \\
& 1 + \sum_{L \in \mathcal{L} \setminus L_T} \exp \left\{ -\frac{n \alpha_L^2}{2\sigma_x^2 (1 - \rho_x)} \right\} \rightarrow 1
\end{aligned} \tag{B.4}$$

The prefactor in Eq. (3.9) diverges since the exponential dominates. If $T = 0$, then Eq. (3.10) will be greater than zero for all sets, L . Thus $d_{\text{TD}}(\mathbf{x}) \rightarrow -\infty$ with $\rho_x \rightarrow 1$.

B.6 Asymptotics for large N

Here we develop asymptotic results for the decision variable when the number of stimuli, N is large. We assume that there a fraction K of the stimuli are targets, so that there are NK targets and $(1 - K)N$ distractors. To simplify notation we write $c_x = \sigma_x^2(1 - \rho_x)$ and $c_s = \sigma_s^2(1 - \rho_s)$. We find that

$$\begin{aligned}
(1 - \rho_s)v_L v &= \frac{c_s}{c_x(c_s + c_x)} \\
v^2 \left(\beta - \frac{1}{\gamma_L} \left(\frac{v_L}{v} \right)^2 \rho_x \sigma_x^2 g_L \right) &= \frac{1}{N} \frac{1}{c_s + c_x} - \frac{1}{NK} \frac{1}{c_x} + O\left(\frac{1}{N^2}\right) \\
v^2 \left(\beta - \frac{1}{\gamma_L} \frac{v_L}{v} \rho_x \sigma_x^2 \right) &= \frac{1}{N} \frac{1}{c_s + c_x} + O\left(\frac{1}{N^2}\right) \\
v^2 \left(\beta - \frac{1}{\gamma_L} f_L \right) &= \left(\frac{1}{N} - \frac{1}{(1 - K)N} \right) \frac{1}{c_x + c_s} + O\left(\frac{1}{N^2}\right) \\
\frac{1 + (\rho_s \sigma_s^2 + \rho_x \sigma_x^2) N v}{\gamma_L} \left(\frac{v_L}{v} \right)^n &= \left(1 + \frac{c_s}{c_x} \right)^{KN} \left(\frac{1}{N} \frac{(\rho_x - 1)(\rho_s \sigma_s^2 + \rho_x \sigma_x^2)}{(K - 1)K \rho_s \rho_x \sigma_s^2} \right)
\end{aligned}$$

We can therefore group the terms in the exponential of the decision variable given by Eq. (3.4) as

$$-\frac{1}{2} \left(\frac{c_s}{c_x(c_s + c_x)} \sum_{i \in L} x_i^2 + \frac{1}{N} \frac{1}{c_x + c_s} \sum_{i,j} x_i x_j - \frac{1}{NK} \frac{1}{c_x} \sum_{i,j \in L} x_i x_j - \frac{1}{(1 - K)N} \frac{1}{c_x + c_s} \sum_{i,j \notin L} x_i x_j \right)$$

A simple reorganization of the terms yields Eq. (3.11).

C Mean stimulus orientation - left or right discrimination task

An observer is presented with N stimuli on every trial. For concreteness, we can think of the stimuli as bars, with orientations $\mathbf{s} = (s_1, s_2, \dots, s_N)$. The task is to decide whether the mean orientation of the set is to the left (a condition we denote by $C = -1$) or right ($C = 1$) of the vertical. The observer makes a decision based on the measurements, $\mathbf{x} = (x_1, x_2, \dots, x_N)$. Stimulus orientations are drawn from a multivariate normal distribution with mean vector, $\mathbf{0}_N$, and covariance matrix, $\mathbf{\Sigma}_s$,

$$p(\mathbf{s}) = \mathcal{N}(\mathbf{0}_N, \mathbf{\Sigma}_s), \quad (\text{C.1})$$

with $\mathbf{\Sigma}_s$ defined in Eq. (2.2). As in the target detection task, we assume the measurements follow a multivariate normal distribution with mean vector and covariance matrix specified in Eq. (2.4).

An ideal observer performs the task by making a decision based on the log posterior ratio,

$$\begin{aligned}
d_{\text{MOD}}(\mathbf{x}) &= \log \frac{p(C = 1|\mathbf{x})}{p(C = -1|\mathbf{x})} = \log \frac{p(\bar{s} > 0|\mathbf{x})}{p(\bar{s} < 0|\mathbf{x})} \\
&= \log \frac{p(\mathbf{x}|\bar{s} > 0)}{p(\mathbf{x}|\bar{s} < 0)} + \log \frac{p(\bar{s} > 0)}{p(\bar{s} < 0)}, \quad (\text{C.2})
\end{aligned}$$

where, $\bar{s} = \sum_{i=1}^N s_i$ denotes the mean stimulus orientation on a trial. If $d_{\text{MOD}}(\mathbf{x}) > 0$, the observer infers $\hat{C} = 1$, that is, the mean stimulus orientation is to the right of the vertical. We compute Eq. (C.2) by marginalizing over \mathbf{s} and applying Bayes' rule,

$$\begin{aligned}
p(\mathbf{x}|\bar{s} > 0) &= \int p(\mathbf{x}|\mathbf{s})p(\mathbf{s}|\bar{s} > 0)d\mathbf{s} \\
&= \int p(\mathbf{x}|\mathbf{s})p(\bar{s} > 0|\mathbf{s})\frac{p(\mathbf{s})}{p(\bar{s} > 0)}d\mathbf{s} \\
&= \frac{1}{p(\bar{s} > 0)} \int_{\bar{s} > 0} p(\mathbf{x}|\mathbf{s})p(\mathbf{s})d\mathbf{s} \\
&= \frac{1}{p(\bar{s} > 0)} \int_{\bar{s} > 0} \mathcal{N}(\mathbf{x}; \mathbf{s}, \Sigma_{\mathbf{x}})\mathcal{N}(\mathbf{s}; \mathbf{0}_N, \Sigma_{\mathbf{s}})d\mathbf{s} \\
&= \frac{z_c}{p(\bar{s} > 0)} \int_{\bar{s} > 0} \mathcal{N}\left(\mathbf{s}; (\mathbf{I} + \Sigma_{\mathbf{x}}\Sigma_{\mathbf{s}}^{-1})^{-1}\mathbf{x}, (\Sigma_{\mathbf{x}}^{-1} + \Sigma_{\mathbf{s}}^{-1})^{-1}\right) d\mathbf{s},
\end{aligned}$$

where z_c is a normalization constant. Similarly, we compute $p(\mathbf{x}|\bar{s} < 0)$ and obtain

$$d_{\text{MOD}}(\mathbf{x}) = \log \left(\frac{\int_{\bar{s} > 0} \mathcal{N}\left(\mathbf{s}; (\mathbf{I} + \Sigma_{\mathbf{x}}\Sigma_{\mathbf{s}}^{-1})^{-1}\mathbf{x}, (\Sigma_{\mathbf{x}}^{-1} + \Sigma_{\mathbf{s}}^{-1})^{-1}\right) d\mathbf{s}}{\int_{\bar{s} < 0} \mathcal{N}\left(\mathbf{s}; (\mathbf{I} + \Sigma_{\mathbf{x}}\Sigma_{\mathbf{s}}^{-1})^{-1}\mathbf{x}, (\Sigma_{\mathbf{x}}^{-1} + \Sigma_{\mathbf{s}}^{-1})^{-1}\right) d\mathbf{s}} \right). \quad (\text{C.3})$$

By symmetry, it is easy to see that the decision boundary in the space of measurements is given by the hyperplane $\bar{x} = 0$, where $\bar{x} = \frac{1}{N} \sum_{i=1}^N x_i$ is the sample mean of the measurement. An ideal observer therefore bases the decision only on the sample mean. Therefore, we have $\bar{x} > 0 \Rightarrow \bar{s} > 0$.

In order to understand the negative impact of noise correlations on the performance of an optimal observer on this task, consider $\mathbf{x} = \mathbf{s} + \vec{\xi}$ where $\vec{\xi} = (\xi_1, \xi_2, \dots, \xi_N) \sim \mathcal{N}(0, \Sigma_{\mathbf{x}})$, so that

$$\bar{x} = \frac{1}{N} \sum_i (s_i + \xi_i) = \bar{s} + \bar{\xi}.$$

In this case, the variance of the mean noise scales with increasing noise correlation strength, ρ_x .

$$\text{Var}(\bar{\xi}) = \frac{\sigma_x^2(1 - \rho_x)}{N} + \rho_x \sigma_x^2.$$

As the variance increases, the overlap between the conditional distributions $p(\bar{x}|\bar{s} > 0)$ and $p(\bar{x}|\bar{s} < 0)$ increases. It is therefore more difficult to tell which condition the measurement comes from, and performance deteriorates.

References

Abbott, L. and Dayan, P. (1999). The effect of correlated variability on the accuracy of a population code. *Neural Computation*, 11(1):91–101.

- Averbeck, B. (2009). *Noise correlations and information encoding and decoding*. Springer.
- Averbeck, B., Latham, P., and Pouget, A. (2006). Neural correlations, population coding and computation. *Nature Neuroscience Reviews*, 7(5):358–366.
- Averbeck, B. and Lee, D. (2006). Effects of noise correlations on information encoding and decoding. *Journal of Neurophysiology*, 95(6):3633–3644.
- Baldassi, S. and Burr, D. C. (2000). Feature-based integration of orientation signals in visual search. *Vision Research*, 40(10):1293–1300.
- Baldassi, S. and Verghese, P. (2002). Comparing integration rules in visual search. *Journal of Vision*, 2(8):3.
- Bartlett, M. (1951). An inverse matrix adjustment arising in discriminant analysis. *The Annals of Mathematical Statistics*, 22(1):107–111.
- Beck, J., Bejjanki, V., and Pouget, A. (2011). Insights from a simple expression for linear Fisher information in a recurrently connected population of spiking neurons. *Neural Computation*, pages 1–19.
- Beck, J., Ma, W., Pitkow, X., Latham, P., and Pouget, A. (2012). Not noisy, just wrong: the role of suboptimal inference in behavioral variability. *Neuron*, 74(1):30–39.
- Berens, P., Ecker, A., Gerwinn, S., Tolias, A., and Bethge, M. (2011). Reassessing optimal neural population codes with neurometric functions. *Proceedings of the National Academy of Sciences of the United States of America*.
- Bhardwaj, M., van den Berg, R., Ma, W., and Josić, K. (2015). Do people take stimulus correlations into account in visual search? *Submitted*.
- Brady, T. and Tenenbaum, J. (2010). Encoding higher-order structure in visual working memory: A probabilistic model. *Proceedings of the 32nd Annual Conference of the Cognitive Science Society*, pages 411–416.
- Chelaru, M. and Dragoi, V. (2008). Efficient coding in heterogeneous neuronal populations. *Proceedings of the National Academy of Sciences of the United States of America*, 105(42):16344–16349.
- Chen, Y., Geisler, W., and Seidemann, E. (2006). Optimal decoding of correlated neural population responses in the primate visual cortex. *Nature Neuroscience*, 9(11):1412–1420.
- Cohen, M. and Kohn, A. (2011). Measuring and interpreting neuronal correlations. *Nature Neuroscience*, 14(7):811–819.
- de la Rocha, J., Doiron, B., Shea-Brown, E., Josić, K., and Reyes, A. (2007). Correlation between neural spike trains increases with firing rate. *Nature*, 448(7155):802–806.
- Ecker, A., Berens, P., Keliris, G., Bethge, M., Logothetis, N., and Tolias, A. (2010). Decorrelated neuronal firing in cortical microcircuits. *Science*, 327(5965):584–587.

- Ecker, A., Berens, P., Tolias, A., and Bethge, M. (2011). The effect of noise correlations in populations of diversely tuned neurons. *The Journal of Neuroscience*, 31(40):14272–14283.
- Ganmor, E., Segev, R., and Schneidman, E. (2011). Sparse low-order interaction network underlies a highly correlated and learnable neural population code. *Proceedings of the National Academy of Sciences*, 108(23):9679–9684.
- Gawne, T. and Richmond, B. (1993). How independent are the messages carried by adjacent inferior temporal cortical neurons? *The Journal of Neuroscience*, 13(7):2758–2771.
- Geisler, W. (2008). Visual perception and the statistical properties of natural scenes. *Annual review of psychology*, 59:167–192.
- Graham, N., Kramer, P., and Yager, D. (1987). Signal-detection models for multidimensional stimuli: Probability distributions and combination rules. *Journal of Mathematical Psychology*, 31(4):366–409.
- Green, D. and Swets, J. (1966). *Signal detection theory and psychophysics*, volume 1. Wiley New York.
- Hansen, B., Chelaru, M., and Dragoi, V. (2012). Correlated variability in laminar cortical circuits. *Neuron*, 76:590–602.
- Harville, D. (1998). Matrix algebra from a statistician’s perspective. *Technometrics*, 40(2):164–164.
- Horn, R. and Johnson, C. (2012). *Matrix analysis*. Cambridge University Press.
- Hu, Y., Zylberberg, J., and Shea-Brown, E. (2014). The sign rule and beyond: boundary effects, flexibility, and noise correlations in neural population codes. *PLoS Computational Biology*, 10(2):e1003469.
- Josić, K., Shea-Brown, E., Doiron, B., and de la Rocha, J. (2009). Stimulus-dependent correlations and population codes. *Neural Computation*, 21(10):2774–2804.
- Kohn, A. and Smith, M. (2005). Stimulus dependence of neuronal correlation in primary visual cortex of the macaque. *The Journal of Neuroscience*, 25(14):3661–3673.
- Latham, P. and Nirenberg, S. (2005). Synergy, redundancy, and independence in population codes, revisited. *The Journal of Neuroscience*, 25(21):5195–5206.
- Latham, P. and Roudi, Y. (2011). Role of correlations in population coding. *arXiv preprint arXiv:1109.6524*.
- Ma, W. (2010). Signal detection theory, uncertainty, and poisson-like population codes. *Vision Research*, 50(22):2308–2319.
- Ma, W., Navalpakkam, V., Beck, J. M., van den Berg, R., and Pouget, A. (2011). Behavior and neural basis of near-optimal visual search. *Nature Neuroscience*, 14(6):783–790.

- Mazyar, H., van den Berg, R., and Ma, W. (2012). Does precision decrease with set size? *Journal of Vision*, 12(6).
- Mazyar, H., van den Berg, R., Seilheimer, R., and Ma, W. (2013). Independence is elusive: set size effects on encoding precision in visual search. *Journal of Vision*, 13(5):1–14.
- Meyer, C. (2000). *Matrix analysis and Applied Linear Algebra Book and Solutions Manual*, volume 2. SIAM.
- Moreno-Bote, R., Beck, J., Kanitscheider, I., Pitkow, X., Latham, P., and Pouget, A. (2014). Information-limiting correlations. *Nature Neuroscience*, 17(10):1410–1417.
- Nolte, L. W. and Jaarsma, D. (1967). More on the detection of one of m orthogonal signals. *Journal of the Acoustical Society of America*, 41(2):497–505.
- Ohiorhenuan, I., Mechler, F., Purpura, K., Schmid, A., Hu, Q., and Victor, J. (2010). Sparse coding and high-order correlations in fine-scale cortical network. *Nature*, 466:617–621.
- Palmer, J., Ames, C. T., and Lindsey, D. T. (1993). Measuring the effect of attention on simple visual search. *Journal of Experimental Psychology: Human Perception and Performance*, 19(1):108.
- Palmer, S. (1999). *Vision science: Photons to phenomenology*, volume 1. MIT press Cambridge, MA.
- Pelli, D. G. (1985). Uncertainty explains many aspects of visual contrast detection and discrimination. *Journal of the Optimal Society of America A*, 2(9):1508–1531.
- Perkel, D., Gerstein, G., and Moore, G. (1967). Neuronal spike trains and stochastic point processes: II. Simultaneous spike trains. *Biophysical Journal*, 7(4):419–440.
- Peterson, W. W., Birdsall, T. G., and Fox, W. (1954). The theory of signal detectability. *Information Theory, Transactions of the IRE Professional Group on*, 4(4):171–212.
- Romo, R., Hernandez, A., Zainos, A., and Salinas, E. (2003). Correlated neuronal discharges that increase coding efficiency during perceptual discrimination. *Neuron*, 38(4):649–657.
- Rosenbaum, R. and Josić, K. (2011). Mechanisms that modulate the transfer of spiking correlations. *Neural Computation*, 23(5):1261–1305.
- Rosenbaum, R., Trousdale, J., and Josić, K. (2010). Pooling and correlated neural activity. *Frontiers in Computational Neuroscience*, 4:9.
- Schneidman, E., Bialek, W., and Berry, M. (2003). Synergy, redundancy, and independence in population codes. *Journal of Neuroscience*, 23(37):11539–11553.
- Seriès, P., Latham, P., and Pouget, A. (2004). Tuning curve sharpening for orientation selectivity: coding efficiency and the impact of correlations. *Nature Neuroscience*, 7(10):1129–1135.

- Shamir, M. and Sompolinsky, H. (2002). Correlation codes in neuronal populations. *Advances in neural information processing systems*, 1:277–284.
- Shamir, M. and Sompolinsky, H. (2006). Implications of neuronal diversity on population coding. *Neural Computation*, 18(8):1951–1986.
- Sherman, J. and Morrison, W. (1950). Adjustment of an inverse matrix corresponding to a change in one element of a given matrix. *The Annals of Mathematical Statistics*, 21(1):124–127.
- Sompolinsky, H., Yoon, H., Kang, K., and Shamir, M. (2001). Population coding in neuronal systems with correlated noise. *Physical Review E*, 64(5):051904.
- Tkačik, G., Prentice, J., Balasubramanian, V., and Schneidman, E. (2010). Optimal population coding by noisy spiking neurons. *Proceedings of the National Academy of Sciences*, 107(32):14419–14424.
- van den Berg, R., Vogel, M., Josić, K., and Ma, W. (2012). Optimal inference of sameness. *Proceedings of the National Academy of Sciences*, 109(8):3178–83.
- Zohary, E., Shadlen, M., and Newsome, W. (1994). Correlated neuronal discharge rate and its implications for psychophysical performance. *Nature*, 370(6485):140–143.